Decoding the dynamic representation of facial expressions of emotion in explicit and incidental tasks

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Abstract

Faces transmit a wealth of important social signals. While previous studies have elucidated the network of cortical regions important for perception of facial expression, and the associated temporal components such as the P100, N170 and EPN, it is still unclear how task constraints may shape the representation of facial expression (or other face categories) in these networks. In the present experiment, we used Multivariate Pattern Analysis (MVPA) with EEG to investigate the neural information available across time about two important face categories (expression and identity) when those categories are either perceived under explicit (e.g. decoding facial expression category from the EEG when task is on expression) or incidental task contexts (e.g. decoding facial expression category from the EEG when task is on identity). Decoding of both face categories, across both task contexts, peaked in time-windows spanning 91-170ms (across posterior electrodes). Peak decoding of expression, however, was not affected by task context whereas peak decoding of identity was significantly reduced under incidental processing conditions. In addition, errors in EEG decoding correlated with errors in behavioral categorization under explicit processing for both expression and identity, but only with incidental decoding of expression. Furthermore, decoding time-courses and the spatial pattern of informative electrodes showed consistently better decoding of identity under explicit conditions at later-time periods, with weak evidence for similar effects for decoding of expression at isolated time-windows. Taken together, these results reveal differences and commonalities in the processing of face categories under explicit Vs incidental task contexts and suggest that facial expressions are processed to a richer degree under incidental processing conditions, consistent with prior work indicating the relative automaticity by which emotion is processed. Our work further demonstrates the utility in applying multivariate decoding analyses to EEG for revealing the dynamics of face perception.

Introduction

Successful categorization of facial expressions of emotion is an important social skill in humans. Hence understanding the neural mechanisms underlying this feat is an important question and the focus of much research. Studies using functional imaging have revealed a network of regions both within and beyond the core face network (Haxby et al., 2000) that show enhanced activity for emotional vs neutral face stimuli (e.g Vuilleumier et al., 2001; Engell and Haxby, 2007). More recently, studies have investigated whether facial expression categories lead to different patterns of brain activity within regions of the face network (see Wegrezyn et al, 2015; Zhang et al, 2016; Greening et al 2018). These studies revealed that particular expression categories can be differentiated in multiple face and emotion brain regions, including superior temporal sulcus (STS - Wegrezyn et al, 2015; Zhang et al, 2016; Greening et al 2018), amygdala (Wegrezyn et al, 2015; Zhang et al, 2016) but also in the fusiform gyrus (FG) and inferior occipital gyrus (IOG) in particular contexts (Wegrezyn et al 2015; see also Greening et al 2018).

Interestingly, two of the aforementioned studies (Wegrezyn et al., 2015; Zhang et al., 2016), used orthogonal tasks which did not require participants to focus on expression to solve the task: i.e. a gender categorization task (Wegrezyn et al) or a fixation task (Zhang et al.), while Greening et al (2018) used an explicit emotion categorization task. Previous activation-based fMRI studies using univariate analyses have shown that the nature of the task performed while viewing facial expressions (i.e. an explicit or incidental expression focus) can have a significant influence on the resulting brain activity observed (esp. e.g. in the amygdala; Critchley et al., 2000; Hariri et al 1999; see also Fusar-Poli et al 2009). However, at present it is still unclear how task may shape the neural representation – indicted via

the multivariate information contained in distributed *brain activity patterns* (Krigeskorte, 2008) - of important face categories, such as facial expression in visual cortex (see Petro et al 2013; Kay & Yeatman, 2017). In the present work, we explicitly address this question using the complementary time-sensitive neuroimaging technique of EEG together with multivariate pattern analysis (MVPA: see Haynes 2015, for a review).

It is well known that neurons in the visual system, even extending back to primary visual cortex, receive significant amounts of top down influence via cortical feedback connections from multiple higher brain regions. It has been argued that these top down influences can effectively change the information conveyed by neurons by, for example, altering their response tuning (Gilbert & Li, 2013). The perceptual task an observer is asked to perform is one such top down influence that can change the activity of neurons in the visual system – even in V1 – to identical visual stimuli (Li et al 2004; Kay & Yeatman, 2017). This in turn allows for boosting of sensory representations that have behavioral relevance in a particular task context (Desimone & Duncan, 1995; see also Peelen et al 2009). While some evidence of task demands altering the response of early visual areas (Li et al 2004; Petro et al 2013) and higher visual areas (Kay & Yeatman, 2017) to identical visual stimuli exist, it is unclear to date how task may shape the dynamically evolving neural representation of important face categories such as expression (and identity).

While studies using fMRI have provided much valuable information about which brain regions code facial expressions, they are necessarily limited in their ability to speak to the time course of neural processing of facial expressions. Much research has been carried out using EEG and MEG, however, to address this question (see e.g. Eimer, 2011). Traditional ERP analyses have demonstrated a specific component related to face processing, the N170, that is thought to be generated in regions of the core face network, i.e. IOG, FG, STS or some combination thereof (see Eimer, 2011). Although the face

sensitivity of the N170 is not in doubt, it is still unclear to what extent this component is sensitive to facial expression. Some studies did not report any sensitivity to emotion in the N170 (e.g. Eimer & Holmes, 2002; Pourtois et al 2005; Eimer & Holmes, 2007; Rellecke, Sommer & Schact, 2013; Neath-Tavares & Itier, 2016) and this is in keeping with a long-standing idea that the N170 indexes structural encoding of a face (see Eimer & Holmes, 2002). Other studies, however, do find some evidence of some sensitivity to emotion on the N170 (Batty & Taylor, 2003; Leppanen et al., 2007, 2008; Schyns et al., 2007; M. Smith 2012; Turano et al 2017) and in fact a recent meta-analysis demonstrates that the N170 is greater for specific emotions (happy, angry and fear) as opposed to neutral (Hinojosa et al 2015). Recent evidence suggests that the earlier discrepancy could in part be driven by methodological differences including both the choice of reference electrodes (with linked mastoids dampening any such effect, Rellecke et al, 2013; Hinojosa et al 2015) and crucially, also by attentional focus (with indirect attention on expression leading to larger effects, Hinojosa et al 2015). In sum, at present it is still unclear to what extent the N170 component may carry discriminative information regarding *each* of the basic facial expressions (i.e. beyond emotion > neutral) across *both* explicit and incidental task contexts. In particular, within-subject designs directly comparing the effect of task on identical stimuli are ideally required to compellingly answer this question (Itier & Neath-Tavares, 2017).

While the N170 has received arguably the most attention as a marker of face processing, visually-evoked components of interest typically begin around the P1, a positivity occurring 100ms post stimulus onset over extra-striate visual regions that is typically linked to low-level stimulus properties and attention (Rossion & Jacques, 2012; Luck et al, 2000). Although early emotion effects have been observed on the P1 in some studies (e.g. Batty & Taylor, 2003; Luo et al 2010; E. Smith et al, 2013), they are by no means consistently observed (see e.g. Itier & Neath-Tavares, 2017; Vulluimier & Pourtois, 2007) and do not necessarily indicate sensitivity to discrete emotions (e.g. though see Luo et al 2010). The early posterior

negativity (EPN) component, occurring around 200-350ms is thought to reflect enhanced processing of emotion in extra-striate areas, likely reflecting feedback from higher brain areas (e.g. Itier & Neath-Tavares, 2017; Recio et al 2017; Pourtois et al 2012; Schupp et al 2003). This component is observed for emotional faces, words and pictures (see Itier & Neath-Tavares, 2017, for review) with higher amplitudes to emotional vs neutral content and is therefore not thought to be face specific per se but rather linked to the encoding of emotional content in general. In particular some studies have found the EPN discriminates valence though not always in a consistent manner (see Itier & Neath-Tavares, 2017 for review). In addition, it has been shown to be sensitive to task demands on identical facial expression stimuli (Itier & Neath-Tavares, 2017). These authors showed that differences between tasks were not evident until 200ms (on lateral occipito-temporal sites) and 300ms (on occipital sites) and showed a different pattern of task effects in each case (Itier & Neath-Tavares, 2017). Thus from the evidence reviewed so far it is not clear whether neural activity encoded within the first 200-300ms post-stimulus will show sensitivity to permit the discrimination of the basic facial expressions of emotion, and whether such sensitivity may be modified by task demands – particularly whether expressions are processed in an explicit vs incidental manner. In the present work we apply more sensitive multivariate analysis techniques (MVPA; see Grootswagers et al 2017, for a review) to determine the neural information contained in the EEG signal about facial expressions (and identities) when processed in an incidental or explicit manner (see Nemrodov et al., 2016).

It is important to point out that a very limited number of prior EEG studies have investigated the effects of task on neural processing of facial expressions using within-subject designs (Itier & Neath-Tavares, 2017; Rellecke et al 2012; Wronka & Walentowska, 2011; DaSilva et al 2016), and they have produced partially contradictory findings. Wronka & Walentowska (2011) found higher N170 for emotional than neutral stimuli but only in an explicit emotion perception task whereas Rellecke et al (2012) found

higher N170 to angry faces in both explicit and incidental emotion perception tasks (they also found emotion > neutral on the later EPN component across both face tasks). Finally we note that DaSilva et al (2016) showed an effect of emotion (happiness and pride) over neutral regardless of task on the N170, while later components such as the P250 showed task influences. Crucially none of these prior studies has investigated what neural information may be contained in the distributed pattern of neural activity for each of the basic expression categories as a function of task with MVPA.

Recently researchers have begun applying multivariate analytic techniques (MVPA) to investigate the dynamic evolution of neural representations revealed by time-sensitive neuroimaging methods, such as EEG or MEG (see Grootswagers et al 2017, for a review). Carlson et al (2013), for instance showed that visual object categories can be decoded from all-channel MEG from around 80-100ms after stimulus onset, and that onset and peak decoding occur earlier for lower (e.g. face Vs object) than higher tier categories (e.g. animate Vs inanimate). Carlson et al (2011), using all-channel MEG, further demonstrated object representations that were invariant to stimulus position by around 200ms. In addition, Cauchoix et al (2014) revealed that faces could be reliably detected within natural scenes at < 100ms and that read out was related to behavior already at 125ms post stimulus. They further argued that the decoding time-course revealed discrete stages of neural information processing. Hence, as these studies show, time-sensitive neuroimaging methods can reveal important insights into the dynamics of visual object and face processing in the brain.

In the present work we combine MVPA decoding with EEG to investigate how task shapes the neural representation of facial expression. Participants completed both an identity and an expression categorization task on the same stimulus set. One hypothesis is that visual representations of faces may be enhanced for task relevant dimensions relatively early, e.g. within the first 200ms, which would lead to enhanced processing of expression in the same expression task, and identity in the identity task at

this time of processing (e.g. Schyns 1998). On the other hand, visual representations may be sensitive to the same stimulus information regardless of task at early time windows, with task sensitivity only emerging later (see e.g. Itier & Neath-Tavares, 2017; M Smith et al 2004). This view would predict that each face attribute (expression or identity) could be discriminated equally across the different tasks within the first 200ms. A third possibility (not mutually exclusive) is that facial expressions may be a specifically salient class of face information (compared to identity or gender) such that they are prioritized for neural processing even when they are not task relevant (e.g. Vuilleumier et al 2001; Anderson et al 2003).

Methods

Subjects

A total of 15 right-handed (via self-report) participants (age range 18-35yrs, 8 female) took part in the present study. Participants were recruited from the undergraduate and postgraduate student population at Birkbeck College and University College London and paid £20 for their participation. All participants gave written, informed consent in accordance with procedures approved by the ethics committee of the School of Psychological Sciences, Birkbeck College, University of London.

Stimuli & Design

Participants completed both a facial expression and an identity recognition task in a single testing session lasting approximately 2 hours. We used 6 faces (3 males, 3 females) from the California Facial Expression database (Dailey et al., 2001) each posing the six basic expressions (Ekman, 1999; happy, sad, fearful, disgusted, angry, and surprised) plus neutral. The same image set of 42 images (6 identities X 7 expressions) was used for both tasks, under different categorization instructions. In the expression task, participants were instructed to categorize the images by facial expression (7AFC: happy, sad, fearful, disgusted, angry, surprised or neutral) by pressing a corresponding key (Z-N) whereas on the identity task, they had to categorize the images by identity (6AFC) by pressing a corresponding key (Z-M). Response keys were not counterbalanced across participants. Images were repeated 20 times per task, for a total of 840 trials per task (120 trials per expression, 140 trials per identity), 1680 trials in total over the course of the testing session. Importantly the identity task was always completed first so as to maximize the chance of expression processing being *incidental* in this case (as our main focus here is on facial expression perception under explicit and incidental task conditions). Participants were introduced

to the six new identities via pictures showing their neutral face, an associated name (Alan, Daniel, Peter, Helen, Louise, Susan) and with two fictitious facts about the person (e.g. in her spare time Louise plays guitar in a folk band).

Each trial began with a fixation cross, presented for 500ms, followed by a face stimulus from the set for 500ms followed by a response interval of 2s. Breaks were interposed every 140 trials in each task (for 6 short blocks per task). A longer break (minimum 10 minutes) separated the two tasks. Participants were seated at a fixed distance of 70cm from a standard CRT monitor (distance fixed by the use of a chin rest), such that the faces spanned 2.54 by 3.84 degrees of visual angle. Participants indicated their categorization choice via labeled keyboard keys. Prior to each task participants completed a short familiarization phase (42 trials) where they practiced the task and the keyboard responses.

EEG Data Acquisition & Analysis

EEG data was recorded from a BrainVision BrainAmp System comprising 64 Ag/AgCl electrodes mounted according to the international 10:20 system in an electrode cap, electrode AFz served as ground and a single mastoid as reference. Horizontal and vertical eye movements were recorded from electrodes positioned at the outer canthi of the eyes (HEOG) and above and below the dominant eye (VEOG). Electrode impedance was lowered to <10kΩ. EEG activity was continually recorded at a sampling rate of 1000Hz (low cutoff 10s, High cutoff 1000Hz). Online software filters had a low cutoff of 10s and a high cutoff of 300Hz (slope 12dB/Octave). EEG data was off-line re-referenced to average reference (excluding the EOG channels), filtered between 0.01 and 35Hz using the built-in EEGLAB function eegfilt which uses two-way least squares FIR (finite impulse response filtering), implemented within the MATLAB signal processing toolbox. Epochs were created around the stimulus onset (-200ms:700ms) for

each trial and baseline corrected using the 200ms prior to stimulus onset. Channels identified as contributing excessive noise to the signal by the automatic EEGLAB routines according to a joint probability estimate of each specific channel (Kurtosis threshold 5) were removed from any further analysis (Identity task: M=4, STD=2, Expression task: M=3, STD=2) and hence not included in any of the MVPA analyses described below. Trials containing artifacts were identified using standard routines in the MATLAB EEGLAB toolbox (Delorme & Makeig, 2004) that remove trials containing large signal values (75 μV threshold). This resulted in the following number of trials being excluded from each task: Identity task: M = 98.1 trials (SD = 97.5, 11.7%), Expression task: M=89.9 (SD = 95, 10.6%).

Multivariate Pattern Classification Analysis (MVPA)

We trained a linear classifier (Linear Support Vector Machine - SVM) to learn the mapping between a set of multivariate EEG observations of brain activity and the particular facial expression (7) or identity (6) that had been presented. We then tested the classifier on an *independent* set of test data. Importantly we decoded both expression and identity from both the expression and identity task data. We used cross-validation to assess the performance of the classifier, with a 70% train to 30% test random split of the data (see Hausfeld et al., 2012; Cauchoix et al., 2014; Tsuchiya et al., 2008) repeated 20 times to form 20 cross-validation iterations (see e.g. Tsuchiya et al 2008). Importantly we sampled the same number of trials per class so as not to bias the classifier (see also Cauchoix et al 2014) and thus note if there were different numbers of trials present in each class (i.e. after EEG preprocessing) we randomly sub-sampled the same number of trials as in the smallest class from each class with a larger number of trials. The training data always consisted of single trial EEG activity patterns while the test

data consisted of an average EEG activity pattern taken across the single trials comprising the test data to increase signal to noise ('average trial analysis', see Smith & Muckli, 2010; Petro et al., 2013). As single trial EEG (or fMRI) data are inherently noisy, averaging across trials can cancel out the noise and hence improve classification performance as we have found empirically for fMRI data (Smith & Muckli 2010; Petro et al 2013; Muckli et al 2015) and we would expect it to do likewise for EEG data (see Grootswagers et al 2017 for a related demonstration with MEG data). The features input to the classifier consisted of the preprocessed EEG voltages from a 60ms wide time window across either all posterior electrodes (all posterior to and including PZ that were not rejected in pre-processing), or all electrodes (that were not rejected in pre-processing and excluding channels used to measure eye movements, see above). Importantly data were never averaged within a given time-window in any of the analyses conducted, only across trials. The analysis was repeated across the whole epoch of the time course by sliding the time window in 10ms offsets (thus the onset of the time windows ranged from -200 to 641ms, with 10ms offsets, giving 85 windows to cover the epoch). We note that this method of *shifting time-windows* has been proposed by some authors to be optimal for revealing the temporal aspects of information processing in the brain (Hausfeld et al 2012).

We tested whether group level decoding accuracy for each time-window was above chance by performing one-tailed t-tests against the chance level of 1/7 or 1/6 (for expression or identity, respectively; see e.g. Smith & Goodale, 2015; Walther et al. 2009; Chen et al. 2011). Control for multiple tests at multiple time windows was implemented by using the False Discovery Rate with $q < .05$ (Benjamini & Hochberg, 1995). The linear SVM algorithm was implemented using the LIBSVM toolbox (Chang and Lin 2011), with default parameters (notably C=1). Note that the activity of each feature in the training data was normalized within a range of -1 to 1 prior to input to the SVM. The test data were normalized using the same parameters (min, max) as obtained from the training set normalization in

order to optimize the classification performance (see Chang and Lin 2011; Smith & Muckli, 2010; Smith & Goodale, 2015; Vetter et al., 2014).

Brain Behavior Correlations

From the decoding analysis above we also extracted a confusion matrix (see e.g. Greening et al 2018; Smith & Goodale 2015; Vetter et al 2014) at each time-window that reveals the pattern of errors made by the classifier (i.e. it reveals the probability of a correct response per class plus the probability of incorrectly assigning each other class, for all classes). For each participant in turn, we correlated the errors in decoding (i.e. the non-diagonal elements of the confusion matrix) for each time-window with the errors that participant made in each categorization task. Note we computed these correlations for each face attribute (expression or identity) under both explicit and incidental processing conditions. Our rationale for computing correlations even under incidental processing was that this would give a measure of the quality of higher level information that is available under these conditions. We used Spearman correlation to mitigate against the risk of outliers affecting the Pearson correlation coefficient (see e.g. Pernet et al., 2012; Greening et al 2018). We Fisher transformed the Spearman rho values to allow averaging across participants. Control for multiple tests across time was again implemented by using the False Discovery Rate with $q < .05$.

Spatially Resolved Classification Analysis

In order to address which electrodes drove classification performance at what time-windows, we performed an additional classification analysis (see e.g. Nemrodov et al., 2016). In this analysis, we ran

the classification analysis as described above except that the analysis was performed independently for each electrode in turn. Thus the features input to the classifier were the EEG signal amplitudes over a given time-window for one particular electrode (see Nemrodov et al., 2016). This allowed us to create a scalp map of where facial expression or identity information can be read out at specific time-windows. We ran this analysis using the same time-window width as the main analyses (i.e. 60ms) but with non-overlapping offsets of 60ms (see also Nemrodov et al 2016). We then computed a spatial map of t-values (one tailed, as above) quantifying where decoding accuracy was significantly above chance (FDR corrected $q < .05$ across electrodes at each time window) for each face property under both explicit and incidental task conditions. We further computed a difference map revealing the spatial locations at which significant differences were present across tasks, independently for each respective face property (again FDR corrected $q < .05$ across electrodes at each time window). We chose this method, as opposed to visualizing the weights of the multi-channel SVM classifier, because the weights of any linear classifier that takes into account interactions between voxels, such as a linear SVM, are typically hard to interpret when projected back into brain space (see Pereira et al 2009; but see also the correction method proposed in Haufe et al., 2014). Note that electrodes marked as bad channels in EEG preprocessing were not included in these analyses, and as such, the number of participants contributing towards the group decoding accuracy varied slightly across electrodes and tasks (mean 14.7, range 13-15).

Results

Analysis of Behavior

Average performance on the expression task reached 69% correct (SD = 10) whereas performance reached 92% correct (SD = 9) on the identity task. As the chance levels were different we did not explicitly compare performance across tasks. The confusion matrices underlying this performance can be seen in Figure 1. For the expression categorization task, a one-way repeated measures ANOVA revealed that the effect of emotion was highly significant, $F(6,84) = 13.72$, $p < .001$, $\eta^2p = 0.495$. Follow-up paired sample t-tests with a Bonferonni correction revealed that happy faces were recognized significantly more accurately than fearful, disgusted, angry and sad faces (all *t*'s > 4.31, *all p*'s < .0007, all *d*'s >= 1.11) while there was a trend for happy faces to be better recognized than both surprised (t (14) = 3.40, p = .0043, d = .88) and neutral faces (t (14) = 3.28, p = .0055, d = .85), which did not survive multiple comparison correction. Neutral faces were recognized significantly better than fearful faces (t(14) = 5.23, p = .0001, d = 1.34) and displayed a trend for better recognition than sad (t (14) = 2.99, p = .0097*, d* = .77) and disgusted faces (t (14) = 2.23, p = .042, d = .58). Disgusted, surprised, angry and sad faces were all better recognized than fearful faces (all *t*'s > 3.90, all *p*'s < .0016, all *d*'s >= 1.01). Thus agreeing with previous research, happy faces were generally the best recognized facial expression (e.g. Smith & Schyns, 2009; Smith & Rossit, 2018).

Decoding Analyses

We computed decoding performance across a sliding time window (60ms long, 10ms offset: see Methods) to reveal how well facial expression (or identity) category can be read out from multi-channel EEG activity, under both explicit and incidental processing conditions (Figure 2). We computed

performance both across all electrodes and for a posterior subset of electrodes (see Methods) as a proxy for those more related to visual processing. We focus on the results obtained with the posterior subset below, but note that a very similar pattern emerged using all electrodes (see Supplementary Figures 1 & 2).

Explicit Decoding of Expression

For decoding of facial expression under explicit conditions (i.e. when participants perform an expression categorization task), decoding was first significant within the 31-90ms time-window and remained significant across almost the entire whole epoch (Figure 2A). We note, moreover, that decoding peaked both in an earlier (91-150 ms) and later time window (611-670ms), with a trough in between. Thus facial expression information contained within the EEG signal does not simply increase monotonically with time, which highlights the possibility of several discrete processing stages being revealed in the decoding time-course (see also Cauchoix et al 2014). Figure 2A, second panel, depicts the confusion matrix underlying this classification performance (averaged across all time windows that led to FDR $q < .05$) and shows that most expressions could be well discriminated except sadness. Figure 2A, third panel, shows the time-windows that led to a significant correlations (averaged across participants) between errors in the neural decoding of expression with errors in behavioural categorization of expression (see Methods). Under explicit processing of expression, significant correlations were evident at three discrete stages of the epoch with onsets of 41, 371 and 571ms respectively.

Incidental Decoding of Expression

We repeated the same analyses (i.e. decoding expression) from the data acquired while participants performed the identity task (Figure 2B). Decoding was first significant within the 41-100ms time

window, and peaked at 111-170ms. It remained significant across the entire epoch although gradually declining across the epoch. Figure 2B, second column, depicts the relevant confusion matrix highlighting that again most expressions are well discriminated, except sadness. Figure 2B, third column, shows the correlation between errors in neural decoding of expression under incidental conditions with errors in participants explicit categorization of expression. This revealed significant correlations were again evident at three discrete stages of the epoch with onsets of 81, 351 and 511ms respectively, indicating a relatively rich representation of expression even under incidental conditions.

Explicit Decoding of Identity

Reliable decoding of identity under explicit task conditions began within the 21-80ms time window and remained significant across the whole epoch (Figure 2C). As in explicit expression decoding, the time course of decoding contained two separate peaks, one in an earlier (101-160ms) and one in a later (591-650ms) time window, with a trough in between. Figure 2C, second column, depicts the confusion matrix underlying this classification, and shows that all identities (6) could be well discriminated. Figure 2C, third column, shows the correlation between errors in neural decoding of identity with errors in participants' categorization of identity. This revealed reliable correlations with onsets at both earlier (onset 31ms) and later (391ms) stages of the epoch.

Incidental Decoding of Identity

Reliable decoding of identity began slightly later within the 41-100ms time window, peaked at 111-170ms time-window, and extended across almost the entire epoch (Figure 2D). However, the decoding magnitude dropped considerably after peaking (from ~40 to ~20% at 451-610ms), but identity read-out rebounded towards the end of the epoch (601-660ms, ~30%). Figure 2D, third column, shows the correlation between errors in neural decoding of identity under incidental conditions with errors in

participants explicit categorization of identity. In this case no reliable correlations could be detected at any time-window (we note a similar pattern is evident on the All Electrode analysis, see Supplementary Text).

Effects of Task on Decoding Expression and Identity

The effect of task on decoding of expression and identity is shown on Figure 3 (A & B respectively). This revealed no significant difference could be detected in decoding expression under explicit or incidental conditions at earlier time periods, only at isolated very late time-windows (Figure 3A: onsets 571-581ms). In contrast, significantly higher decoding of identity under explicit conditions was present in both earlier (Figure 3B: onsets at 91-121ms, 161-181ms and 271-281ms) and later time periods (onsets from 351 – 591ms). Importantly this analysis demonstrates that peak decoding of identity is weaker under incidental processing.

To complement this analysis, we also conducted a further analysis where peak decoding was defined in a subject-specific manner (computed per participant across time-window onsets covering 50 – 200ms, see Methods). Figure 3C shows the single participant data underlying these analyses in the form of a strip-chart (see e.g. Rousselet et al 2017). These analyses revealed no change in peak decoding of expression as a function of task ($t(14) = 0.53$, $p = .61$, two-tailed; $d = 0.14$; Explicit = 24%, Incidental = 25%) but a significant decline in decoding of identity in the incidental task ($t(14) = 3.66$, $p = .0026$, two-tailed; $d = .95$; Explicit = 39%, Incidental = 32%). Thus these results again reveal that identity information is not as well represented during incidental conditions whereas no difference could be detected in peak decoding of expression as a function of task (i.e. explicit Vs incidental).

We note that the same pattern of results is present if we use all electrodes rather than just the posterior subset for both the analyses of task effects considered here – see Supplementary Figures 1 & 2.

Spatially-Resolved Decoding of Face Information

In order to investigate which specific electrodes may be contributing to the successful decoding reported above, we re-ran our classification analyses independently per electrode using the same time-window length (60ms; see Nemrodov et al, 2016). Figures 4 and 5 shows the results of these analyses.

In explicit decoding of expression (Figure 4A), central electrodes showed significant decoding initially, although there were strong trends present at posterior sites in the same (161-220ms) and earlier (101-160ms) time windows, which did not survive multiple comparison correction. By 221-280ms posterior, central and frontal electrodes all showed reliable decoding of expression. Reliable decoding was again present at 401-460ms and from 521-580ms onwards, presumably for response related read-out.

In incidental decoding of expression (Figure 4B), initially (41-100ms, 101-160ms) posterior electrodes showed the most robust decoding. Between 221-280ms robust decoding was present at frontal sites, in addition to some central and many posterior electrodes. Significant decoding was absent from onsets of 401ms onwards.

Furthermore, there were no significant effects of task on decoding expression (Figure 4C), except one isolated frontal electrode which showed higher decoding of expression under explicit task conditions in the final time window (640-700ms). This concurs with the main decoding analyses reported earlier, in that no effects of task on expression decoding were detected in earlier time periods, only during very late, likely response related, stages of the epoch.

For explicit decoding of identity (Figure 5A), initially posterior sites showed most robust decoding (41-100ms) before gradually moving bilaterally and anteriorly (101-160ms). From 341-400ms time window onwards, very robust decoding was present throughout most of the scalp. For incidental decoding of identity (Figure 5B), on the other hand, decoding was robustly present at posterior and central sites initially (101-160ms) and then became more robust at frontal sites (161-220ms time-windows). Decoding was largely absent from 341-580ms onwards but was significant again at 581-640ms onwards, mirroring the pattern seen in the main decoding timecourse analyses (Figure 2D).

Significant effects of task on decoding identity was found from 401-460ms time window onwards (Figure 5C), demonstrating that identity information was better decodable under explicit than incidental processing conditions (including over posterior sites), which again concurs with our main decoding analyses reported earlier. Thus task affects neural coding of identity at late stages of processing over posterior sites. Notably however no effects of task on decoding identity were detected at earlier time periods in these single channel analyses, highlighting the likely increased sensitivity gained by combining data across electrodes in our main analyses (Grootswagers et al 2017; Haynes 2015).

Discussion

In the present study we investigated how task shapes neural representations of facial expression and facial identity, using EEG with MVPA. Our findings show that peak decoding for expression is not affected by task set whereas peak decoding of identity is affected by task set. Moreover decoding of identity is better under explicit conditions at multiple points across the entire decoding time-course, whereas decoding of expression was only better under explicit conditions at very late time periods. We report reliable correlations of the errors in neural decoding with errors in human categorization at both earlier and later periods during explicit tasks but only for expression in an incidental task. Finally, spatially-resolved decoding analyses further revealed better decoding of identity under explicit task conditions but only at later time periods (400ms post-stimulus).

Incidental task context weakens peak decoding of identity but not expression

We report reliably greater decoding of identity when identity is task relevant than task-irrelevant (i.e. decoding identity in the identity vs expression task), across two independent analyses within the first 200ms (incorporating the time periods of the traditional P1 and N170 ERP components). However, for expression, we did not find any difference as a function of task (i.e. decoding expression in the expression vs identity task) until very late in the decoding time-course (571ms post-stimulus). These findings are consistent with two accounts of how task shapes visual processing of face categories. First, the change of performance for identity may be due to top down attentional mechanisms boosting processing of identity when it is a task relevant dimension comparable to effects reported in early visual areas for simpler dimensions (see e.g. Maunsell, 2015) and to those recently reported in face areas for

identity (Gratton et al., 2013; see also Kay & Yeatman, 2017). This is also consistent with the greater BOLD responses observed in ventral regions for attending to identity Vs expression, whereas STS shows the opposite pattern (see Hoffman & Haxby 2000). Such effects of attention on high level visual regions may be driven by regions in the IPS (Kay & Yeatman, 2017).

If we assume the same account applies to expression perception, then this would imply that the failure to find a significant difference for expression across tasks, is due to the absence of such top down mechanisms operating during explicit expression decoding within the first 200ms. That is, expression perception would be determined by the same bottom-up stimulus processing in both cases. However there are several reasons why we do not think this is the case: First, top-down influences on emotion perception are known to occur and generate feedback to visual cortex (e.g. Furl et al 2013; Vuilleumier et al 2004). Second, we found reliable correlations of the incidental neural representation of emotion with participants' explicit emotion perception– implying that a relatively rich representation of emotion is constructed even when emotion is non-task relevant. In fact, a long-standing body of work on emotion and attention, has revealed that it is difficult to ignore the emotion presented in sensory stimuli, unless attention is very highly loaded on a different attribute: something that would be rather unlikely given the present experimental design (see e.g. Pessoa & Ungerleider, 2004; Phelps et al 2006).

Hence we argue that due to the evolutionary importance of facial expressions as high-value signals - that transmit information about the mental states, intentions and environment of the expresser (Darwin 1872; Fridlund,1994; Matsumoto, 2001) - relative to that of facial identity signals – our results may actually reveal no difference in the early neural processing of expressions in explicit and incidental task contexts *because* emotions are preferentially processed even in incidental task contexts, whereas facial identities are not (perhaps particularly in the case of very simply and recently learned identities as used in the present experiment). While previous neuroimaging studies have revealed that different brain

areas may be active in incidental Vs explicit emotion perception, overall the pattern is still unclear and in need of further investigation (e.g. Critchley et al., 2000; Chi-Hua Chen et al., 2006; Hariri et al 1999; Lange et al., 2006; but see also Gur et al 2002).

A recent fMRI study (Dobs et al 2018), however, directly addressed how task shapes neural representation of facial expression and identity revealed that surprisingly, both early visual areas (V1-V4) and STS discriminated facial expressions better when participants performed an expression task, while both FFA and STS showed better decoding of identity in an identity task. Thus in this case, clear effects of task shaping visual representations were found for both face attributes, albeit in different brain areas. While the Dobs et al study is admirable for equating task difficulty and stimulus differences precisely across key comparisons, the study used quite a limited set of facial expressions (just angry and happy) and facial identities (two females), and employed stimuli that are clearly artificial. Hence it is unclear to what extent the findings are truly generalizable across different expression categories in the different task contexts (here, we use the full set of six basic expressions plus neutral, and six identities comprising both males and females). Future studies, in any case, will be necessary to reveal the extent to which facial expressions may be preferentially encoded independent of task.

Identity and Expression were maximally decodable within time-windows centered around 100ms over posterior electrodes

Despite the key difference noted above in how task set affected peak decoding for expression vs identity, there were similarities in the overall shape of decoding time-courses for each face attribute when perceived in explicit Vs incidental task contexts. First, decoding was maximal in a 90-170ms time-period post-stimulus with very slight differences due to task and face attribute. Thus for the posterior

set of electrodes used in our main analyses (posterior to and including Pz), this demonstrates that maximal face information about identity and expression is present around 90-170ms post-stimulus time-window. Previous work has revealed that read-out of face exemplar information from whole brain MEG is present across an ~ 80-200ms time-period (Carlson et al 2013; see also Carlson et al., 2011). In addition, Nemrodov et al (2016), revealed a clear peak in decoding around 150ms for decoding both face identity and gender from all scalp EEG (initial smaller peak at 70ms). Thus the present findings are in broad agreement with the limited previous literature that has attempted to decode fine-grained properties about human faces from high temporal resolution neuroimaging techniques. Importantly the present study goes beyond this literature by systematically quantifying the information available about both the expression and identity of human faces across time, in both explicit and incidental task contexts.

Decoding of identity was better under explicit than incidental conditions at later time-periods in both the decoding time-course and in the spatially-resolved analyses

Decoding of identity under explicit task conditions was also consistently higher than such decoding under incidental conditions at later time periods (onsets between 351 and 591ms). This phase of the decoding time-course may reflect the maintenance of the available face information in higher level visual areas important in face processing such as OFA, FFA and STS in preparation for response related read-out (see e.g. Cauchoix et al 2014). Importantly a similar pattern was also apparent in the spatially-resolved analyses where reliable effects of task on decoding of identity were seen from 400ms post-stimulus onwards across posterior, but also central and frontal, sites. On the other hand, effects of task on decoding of expression were only sparsely present at very late time-windows in both the main

decoding analyses (591ms onset) and also in the spatially-resolved analyses (641ms onset, single electrode). Thus while effects of task on decoding of expression were sparse at later time-periods, they were in the same direction as found for identity: i.e. better decoding under explicit than incidental task conditions (we note that somewhat stronger effects of task on decoding of expression were present on the analysis using all electrodes at later time-periods). This suggests that at least at some later time-periods effects of task may act to maintain the sensory representation of both face categories for response-related processing (Cauchoix et al., 2014).

Conclusion

In summary, the present study reveals robust effects of task context on both earlier and later stages of neural processing of face identity but only weak effects of task at late stages for expression. This suggests that facial expressions are processed to a richer degree even under incidental processing conditions, consistent with prior work indicating the relative automaticity by which emotion is processed. Our results further demonstrate evidence of discrete processing stages in the dynamically evolving representation of two important face categories in visual cortex. Finally our work shows the utility in applying multivariate decoding analyses to EEG for revealing the dynamics of face perception.

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References

Anderson AK, Christoff K, Panitz D, De Rosa E, Gabrieli JDE. (2003). Neural correlates of the automatic processing of facial threat signals. *Journal of Neuroscience*, 23, 5267-5633.

Batty, M., & Taylor, M. J. (2003). Early processing of the six basic facial emotional expressions. *Cognitive Brain Research, 17*(3), 613-620. doi:http://dx.doi.org/10.1016/S0926-6410(03)00174-5

Carlson TA, Hogendoorn H, Kanai R, Mesik J, Turret J. (2011). High temporal resolution decoding of object position and category. *Journal of Vision*, 11, 9.

Carlson TA, Tovar DA, Alink A & Kriegeskorte N. (2013). Representational dynamics of object vision: The first 1000ms. *Journal of Vision*, 13, 1.

Cauchoix, M., Barragan-Jason, G., Serre, T., & Barbeau, E. J. (2014). The neural dynamics of face detection in the wild revealed by MVPA. *J Neurosci, 34*(3), 846-854. doi:10.1523/JNEUROSCI.3030-13.2014

Chang CC, Lin CJ. 2011. LIBSVM: a library for support vector machines. *ACM Transactions on Intelligent Systems and Technology* 2:27.

Chen Y, Namburi P, Elliott LT, Heinzle J, Soon CS, Chee MW, Haynes JD. 2011. Cortical surface-based searchlight decoding. Neuroimage. 56:582-592.

Critchley, H., Daly, E., Phillips, M., Brammer, M., Bullmore, E., Williams, S., . . . Murphy, D. (2000). Explicit and neural mechanisms for processing of social information from facial expressions: A functional magnetic resonance imaging study. *Hum Brain Mapp, 9*(2), 93-105. doi:10.1002/(SICI)1097-0193(200002)9:2<93::AID-HBM4>3.0.CO;2-Z

Darwin C. (1872). *The expression of emotion in man and animals.* New York, NY: Oxford University Press.

DaSilva EB, Crager K & Puce A. (2016). On dissociating the neural time course of the processing of positive emotions. *Neuropsychologia*, 83, 123-137.

Delorme, A. & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. Journal of Neuroscience Methods, 134(1), 9-21.

Desimone R, Duncan J. (1995). Neural mechanisms of selective visual attention. *Annual Reviews Neuroscience*, 18, 193-222.

Dobs K, Schultz J, Bulthoff I, Gardner JL. (2018). Task-dependent enhancement of facial expression and identity representations in human cortex. *Neuroimage*, 172, 689-702.

Eimer, M., & Holmes, A. (2002). An ERP study on the time course of emotional face processing. *NeuroReport, 13*(4), 427-431.

Eimer, M., & Holmes, A. (2007). Event-related brain potential correlates of emotional face processing. *Neuropsychologia, 45*(1), 15-31. doi:10.1016/j.neuropsychologia.2006.04.022

Eimer M. (2011). The face-sensitive N170 component of the event-related brain potential. In Calder AJ et al (eds). *The Oxford Handbook of Face Perception*. Oxford University Press.

Engell AD, Haxby JV (2007) Facial expression and gaze-direction in human superior temporal sulcus. Neuropsychologia 45:3234-3241.

Fridlund A. (1994). *Human Facial Expression*: *An evolutionary view*. San Diego, CA: Academic Press.

Fusar-Poli P, Placentino A, Carletti F, Landi P, Allen P, Surguladze S, Benedetti F, Abbamonte M, Gasparotti R, Barale F, Perez J, McGuire P, Politi P (2009) Functional atlas of emotional faces

processing: a voxel-based meta-analysis of 105 functional magnetic resonance imaging studies. J Psychiatry Neurosci 34:418-432.

Furl N, Henson RN, Friston KJ, Calder AJ (2013) Top-down control of visual responses to fear by the amygdala. J Neurosci 33:17435-17443.

Gilbert CD, Li W. (2013). Top-down influences on visual processing. *Nature Reviews Neuroscience*, 14, 350-363.

Gratton C, Sreenivasan KK, Silver MA, D-Epsposito M. (2013). Attention selectively modifies the representation of individual faces in the human brain. *Journal of Neuroscience*, 33, 6979-6989.

Greening, S. G., Mitchell, D. G. V., & Smith, F. W. (2018). Spatially generalizable representations of facial expressions: Decoding across partial face samples. *Cortex, 101*, 31-43. doi:https://doi.org/10.1016/j.cortex.2017.11.016

Grootswagers, T., Wardle, S. G., & Carlson, T. A. (2017). Decoding Dynamic Brain Patterns from Evoked Responses: A Tutorial on Multivariate Pattern Analysis Applied to Time Series Neuroimaging Data. *Journal of Cognitive Neuroscience, 29*(4), 677-697. doi:10.1162/jocn_a_01068

Gur RC, Schroeder L, Turner T, McGrath C, Chan RM et al. (2002). Brain activation during facial emotion processing. *Neuroimage*, 16, 651-662.

Hariri, A. R., Bookheimer, S. Y., & Mazziotta, J. C. (2000). Modulating emotional responses: effects of a neocortical network on the limbic system. *NeuroReport, 11*(1), 43-48.

Hausfield L, De Martino F, Bonte M & Formisano E. (2012). Pattern analysis of EEG responses to speech and voice: influence of feature grouping. *Neuroimage*, 59, 3641-3651.

Haxby JV, Hoffman EA, Gobbini MI (2000) The distributed human neural system for face perception. Trends Cogn Sci 4:223-233.

Haufe S, Meinecke F, Gorgen K, Dahne S, Haynes JD et al. (2014). On the interpretation of weight vectors of linear models in multivariate neuroimaging. *Neuroimage*, 87, 96-110.

Hinojosa, J. A., Mercado, F., & Carretié, L. (2015). N170 sensitivity to facial expression: A meta-analysis. *Neuroscience & Biobehavioral Reviews, 55*, 498-509. doi:http://dx.doi.org/10.1016/j.neubiorev.2015.06.002

Hoffman EA, Haxby JV. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience*, 3, 80-84.

Kay KN, Yeatman, JD. (2017). Bottom-up and top-down computations in word- and face-selective cortex. *eLife*, 6:e22341 doi: 10.7554/eLife.22341.

Kriegeskorte N, Mur M, Bandettini P. (2008). Representational similarity analysis – connecting the branches of system neuroscience. *Front. Syst. Neurosci.* **2**:4. doi: 10.3389/neuro.06.004.2008.

Leppänen, J. M., Hietanen, J. K., & Koskinen, K. (2008). Differential early ERPs to fearful versus neutral facial expressions: A response to the salience of the eyes? *Biological Psychology, 78*(2), 150-158. doi:https://doi.org/10.1016/j.biopsycho.2008.02.002

Li W, Piech V, Gilbert CD. (2004). Perceptual learning and top-down influences in primary visual cortex. *Nature Neuroscience*, 7, 651-657.

Luck SJ, Woodman GF, Vogel EK. (2000). Event-related potential studies of attention. Trends in Cognitive Sciences. 4(11), 432–440.

Luo W, Feng W, He W, Wang N, Luo Y. (2010). Three stages of facial expression processing: ERP study with rapid serial visual presentation. *Neuroimage*, 49, 1857-1867.

Maunsell, JHR. (2015). Neuronal mechanisms of visual attention. *Annual Review Vision Science*, 1, 373-391.

Matsumoto D, Hwang RS. (2011). Judgments of facial expressions of emotion in profile. *Emotion*, 11, 1223–1229.

Neath-Tavares, K. N., & Itier, R. J. (2016). Neural processing of fearful and happy facial expressions during emotion-relevant and emotion-irrelevant tasks: A fixation-to-feature approach. *Biological Psychology, 119*(Supplement C), 122-140. doi:https://doi.org/10.1016/j.biopsycho.2016.07.013

Nemrodov, D., Niemeier, M., Mok, J. N. Y., & Nestor, A. (2016). The time course of individual face recognition: A pattern analysis of ERP signals. *Neuroimage, 132*, 469-476. doi:https://doi.org/10.1016/j.neuroimage.2016.03.006

Peelen MV, Fei Fei L, Kastner S. (2009). Neural mechanisms of rapid natural scene categorization in human visual cortex. *Nature*, 460, 94-97.

Pereira F, Mitchell T, Botvinick M. (2009). Machine learning classifiers and fMRI: a tutorial overview. *Neuroimage*, 45, S199-S209.

Pernet CR, Wilcox R, Rousselet GA (2012) Robust correlation analyses: false positive and power validation using a new open source Matlab toolbox. Frontiers in psychology 3.

Petro LS, Smith FW, Schyns PG, Muckli L (2013) Decoding face categories in diagnostic subregions of primary visual cortex. Eur J Neurosci 37:1130-1139.

Pessoa L, Ungerleider LG. (2004). Neuroimaging studies of attention and the processing of emotion-laden stimuli. *Prog. Brain Research*, 144, 171-182.

Phelps EA, Ling S, Carrasco M. (2006). Emotion facilitates and potentiates the perceptual benefits of attention. *Psychological Science*, 17, 292-299.

Pourtois G, Dan ES, Grandjean D, Sander D, Vuilleumier P. (2005). Enhanced extrastriate visual response to bandpass: time course and topographic evoked potentials mapping. *Human Brain Mapping* 26, 65–79.

Recio G, Wilhelm O, Sommer W, Hildebrandt A. (2017). Are event-related potentials to dynamic facial expressions of emotion related to individual differences in the accuracy of processing facial expressions and identity? *Cogn. Affect. Behav. Neurosci*. 17, 364–380. 10.3758/s13415-016-0484-6

Rellecke J, Sommer W, Schacht A. (2012). Does processing of emotional facial expressions depend on intention? Time-resolved evidence from event-related brain potentials. *Biological Psychology*, 90, 23–32.

Rossion B, Jacques C. (2012). The N170: Understanding the time course of face perception in the human brain. In: Luck, S.J., Kappenman, E.S. (Eds.), *The Oxford Handbook of Event-Related Potential Components*. Oxford University Press, Oxford, pp. 115–141.

Rousselet GA, Pernet CR, & Wilcox RR. (2017). Beyond differences in means: robust graphical methods to compare two groups in neuroscience. The European Journal of Neuroscience, 74, 603.Schyns PG. (1998). Diagnostic recognition: task constraints, object information, and their interactions. *Cognition,* 67, 147-179.

Schyns, P. G., Petro, L. S., & Smith, M. L. (2007). Dynamics of Visual Information Integration in the Brain for Categorizing Facial Expressions. *Current Biology, 17*(18), 1580-1585. doi:10.1016/j.cub.2007.08.048

Schupp HT, Junghofer M, Weike AI, Hamm AO. Emotional facilitation of sensory processing in the visual cortex. *Psych Science*, 1, 7-13.

Smith E, Weinberg A, Moran T, Hajcak G. (2013). Electrocortical responses to NIMSTIM facial expressions of emotion. *Int. J. Psychophysiology*, 88, 17-25.

Smith FW, Schyns PG. (2009). Smile through your fear and sadness: transmitting and identifying facial expression signals over a range of viewing distances. *Psychological Science, 20*(10), 1202-1208.

Smith FW, Muckli L (2010) Nonstimulated early visual areas carry information about surrounding context. Proc Natl Acad Sci U S A 107:20099-20103

Smith FW, Goodale MA (2015) Decoding visual object categories in early somatosensory cortex. Cereb Cortex 25:1020-1031.

Smith FW, Rossit S. (2018). Identifying and detecting facial expressions of emotion in peripheral vision. *PLOS ONE*, 13: e0197160, doi: 10.1371/journal.pone.0197160

Smith, M. L., Gosselin, F., & Schyns, P. G. (2004). Receptive Fields for Flexible Face Categorizations. *Psychological Science, 15*(11), 753-761. doi:10.1111/j.0956-7976.2004.00752.x

Smith, M. L. (2012). Rapid Processing of Emotional Expressions without Conscious Awareness. *Cerebral Cortex*, 8, 1748-1760.

Turano, M. T., Lao, J., Richoz, A.-R., Lissa, P. d., Degosciu, S. B. A., Viggiano, M. P., & Caldara, R. (2017). Fear boosts the early neural coding of faces. *Social Cognitive and Affective Neuroscience, 12*(12), 1959-1971. doi:10.1093/scan/nsx110

Tsuchiya N, Kawasaki H, Oya H, Howard MA, 3rd, Adolphs R (2008) Decoding face information in time, frequency and space from direct intracranial recordings of the human brain. PLoS One 3:e3892.

Vetter, P., Smith, F.W., & Muckli, L. (2014). Decoding sound and imagery content in early visual cortex. *Current Biology*. 24, 1256-1262.

Vuilleumier P, Armony J, Driver J, Dolan RJ. (2001). Effects of attention and emotion on face processing in the human brain: an fMRI study. *Neuron*, 30, 829-841.

Vuilleumier P, Richardson MP, Armony JL, Driver J, Dolan RJ (2004) Distant influences of amygdala lesion on visual cortical activation during emotional face processing. Nat Neurosci 7:1271-1278.

Vuilleumier P, Pourtois G. (2007). Distributed and interactive brain mechanisms during emotion face perception: Evidence from functional neuroimaging. *Neuropsychologia* 45, 174–194.

Walther DB, Caddigan E, Fei-Fei L, Beck DM. 2009. Natural scene categories revealed in distributed patterns of activity in the human brain. J. Neurosci. 29:10573-10581.

Wegrzyn M, Riehle M, Labudda K, Woermann F, Baumgartner F, Pollmann S, Bien CG, Kissler J (2015) Investigating the brain basis of facial expression perception using multi-voxel pattern analysis. Cortex 69:131-140.

Wronka, E., & Walentowska, W. (2011). Attention modulates emotional expression processing. *Psychophysiology, 48*(8), 1047-1056. doi:10.1111/j.1469-8986.2011.01180.x

Zhang H, Japee S, Nolan R, Chu C, Liu N, Ungerleider LG (2016) Face-selective regions differ in their ability to classify facial expressions. Neuroimage 130:77-90.

Figure 1: Human Categorization Performance

A) Confusion matrix pertaining to Expression Task. Rows represent expression category and columns represent the response chosen by the participant (N=Neutral, H=Happy, Su.=Surprise, F=Fear, D=Disgust; A=Anger; Sa.=Sad). The diagonal hence represents correct responses, and the off diagonal errors. The colour scale indicates the percentage of times a particular stimulus and response pair were chosen on average across participants.

B) As in A) but for the Identity Task. Rows and columns here hence represent identity (M=Male, F=Female).

Figure 2: Decoding of Facial Expression and Facial Identity in Explicit and Incidental Tasks

A) Left Panel: Decoding of facial expression in explicit task (while participants categorized the faces by expression) for each time-window (60ms wide, 10ms offsets, covering the whole epoch). Red stars represent significant decoding FDR corrected $q < .05$ (chance =14.29%, solid black line). Blue circles represent uncorrected $p < .001$. Middle panel: Confusion matrix pertaining to the decoding results at left, averaged across all time-windows that led to FDR corrected significant decoding. Rows represent expression category and columns the response chosen by the decoder. The diagonal hence represents correct decisions and the off-diagonal reflects the errors made by the decoder. Right Panel: Average Spearman correlation (across participants) between errors in human behavioral categorization of expression and errors in decoding.

B) As above but for incidental decoding of facial expression (i.e. decoding identity while participants categorized the faces by identity). Chance = 14.29%.

C) As above but for explicit decoding of identity (i.e. decoding identity while participants categorized the faces by identity). Chance = 16.67%.

D) As Above but for incidental decoding of identity (i.e. decoding identity while participants categorized the faces due to expression). Chance =16.67%.

Figure 3: Effects of Task on Decoding Expression and Identity

A) Decoding accuracy for expression in both explicit (green) and incidental (blue) task contexts is shown together with the difference (explicit – incidental: gray line, black dashed line represents 1 standard error of the mean). Red stars represent a significant difference in decoding at FDR corrected at $q < .05$ (two-tailed t-test).

B) As in A but for decoding of identity.

C) Strip-chart showing single participant peak decoding accuracies for decoding each face property (ID=Identity; Expr=Expression) in both task contexts (Exp. = Explicit; Inc. = Incidental). Peak decoding accuracy was computed independently per participant across 0-200ms time-window onsets (see Methods and Results).

Figure 4: Spatially-Resolved Decoding of Facial Expression in Explicit and Incidental Tasks

A) Decoding of facial expression in the explicit task. Each map shows the t-values for whether decoding is above chance at each electrode for a given time-window. Blue stars indicate FDR corrected $q < .05$.

B) As in A, but for decoding of facial expression in the incidental (identity) task.

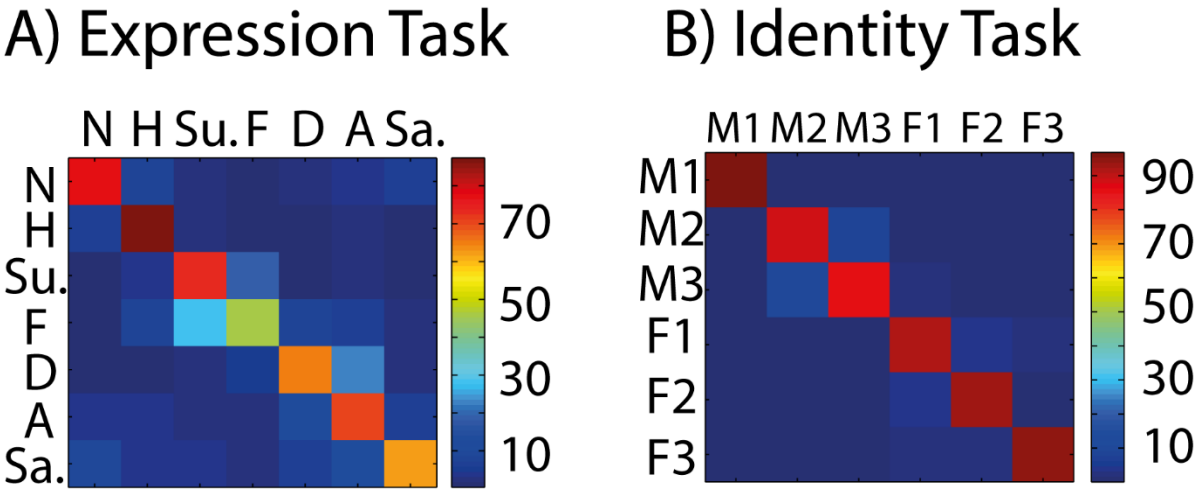
C) Difference in decoding expression in explicit and incidental tasks (explicit – incidental). Each map shows the t-values for where there is a significant difference between decoding performance across the two tasks. Blue stars indicate FDR corrected $q < .05$.

Figure 5: Spatially-Resolved Decoding of Facial Identity in Explicit and Incidental Tasks

A) Decoding of facial identity in the explicit (identity) task. Each map shows the t-values for whether decoding is above chance at each electrode for a given time-window. Blue stars indicate FDR corrected $q < .05$.

B) As in A, but for decoding of facial identity in the incidental (expression) task.

C) Difference in decoding identity in explicit and incidental tasks (explicit – incidental). Each map shows the t-values for where there is a significant difference between decoding performance across the two tasks. Blue stars indicate FDR corrected $q < .05$.


A) Expression Task
N H Su. F D A Sa.
N
H
Su.
F
D
A
Sa.
70
50
30
10
B) Identity Task
M1 M2 M3 F1 F2 F3
M1
M2
M3
F1
F2
F3
90
70
50
30
10

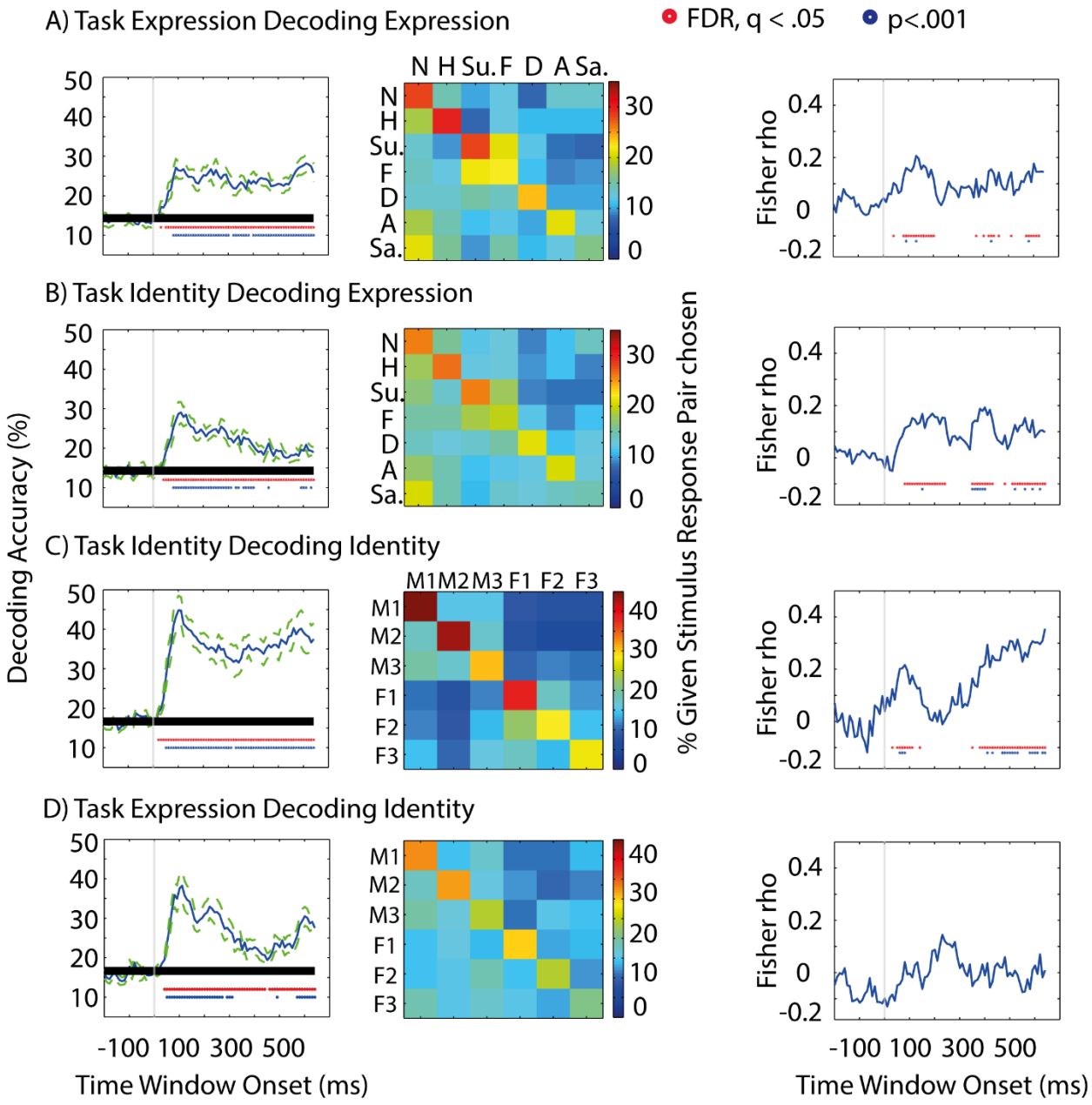

A) Task Expression Decoding Expression
FDR, q < .05
p<.001
N H Su. F D A Sa.
B) Task Identity Decoding Expression
C) Task Identity Decoding Identity
M1 M2 M3 F1 F2 F3
D) Task Expression Decoding Identity
Decoding Accuracy (%)
% Given Stimulus Response Pair chosen
Fisher rho
-100 100 300 500
Time Window Onset (ms)

Figure 2

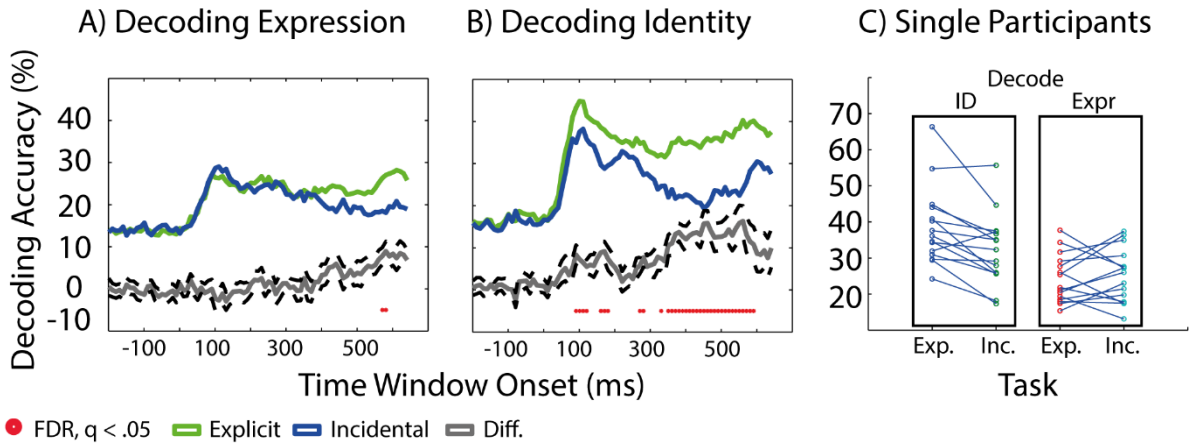

A) Decoding Expression
B) Decoding Identity
C) Single Participants
Decoding Accuracy (%)
40
30
20
10
0
-10
-100
100
300
500
Time Window Onset (ms)
Decode
ID
Expr
70
60
50
40
30
20
Exp.
Inc.
Exp.
Inc.
Task
FDR, q < .05
Explicit
Incidental
Diff.

Figure 3

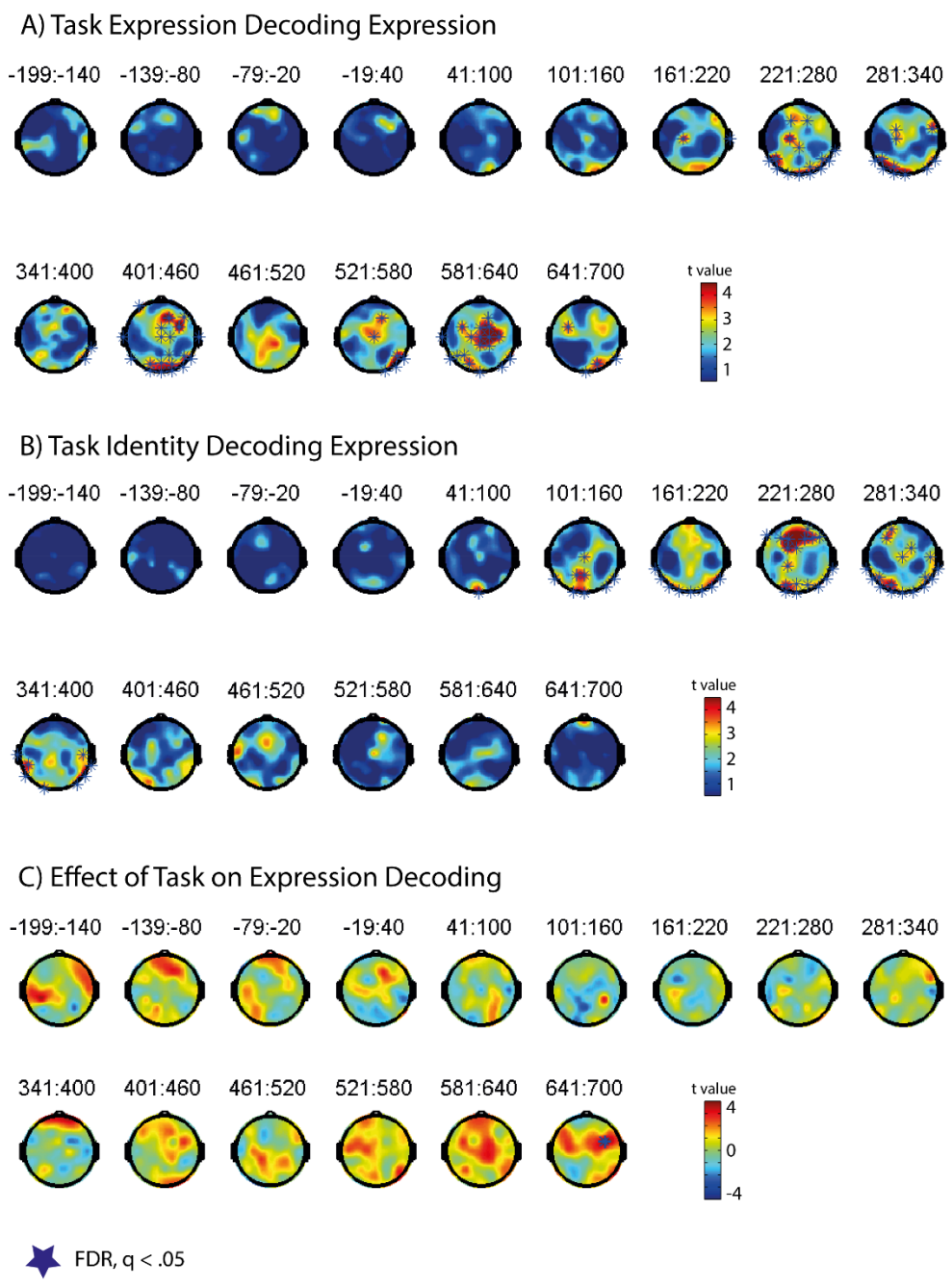


Figure 4: Spatially resolved expression decoding across tasks

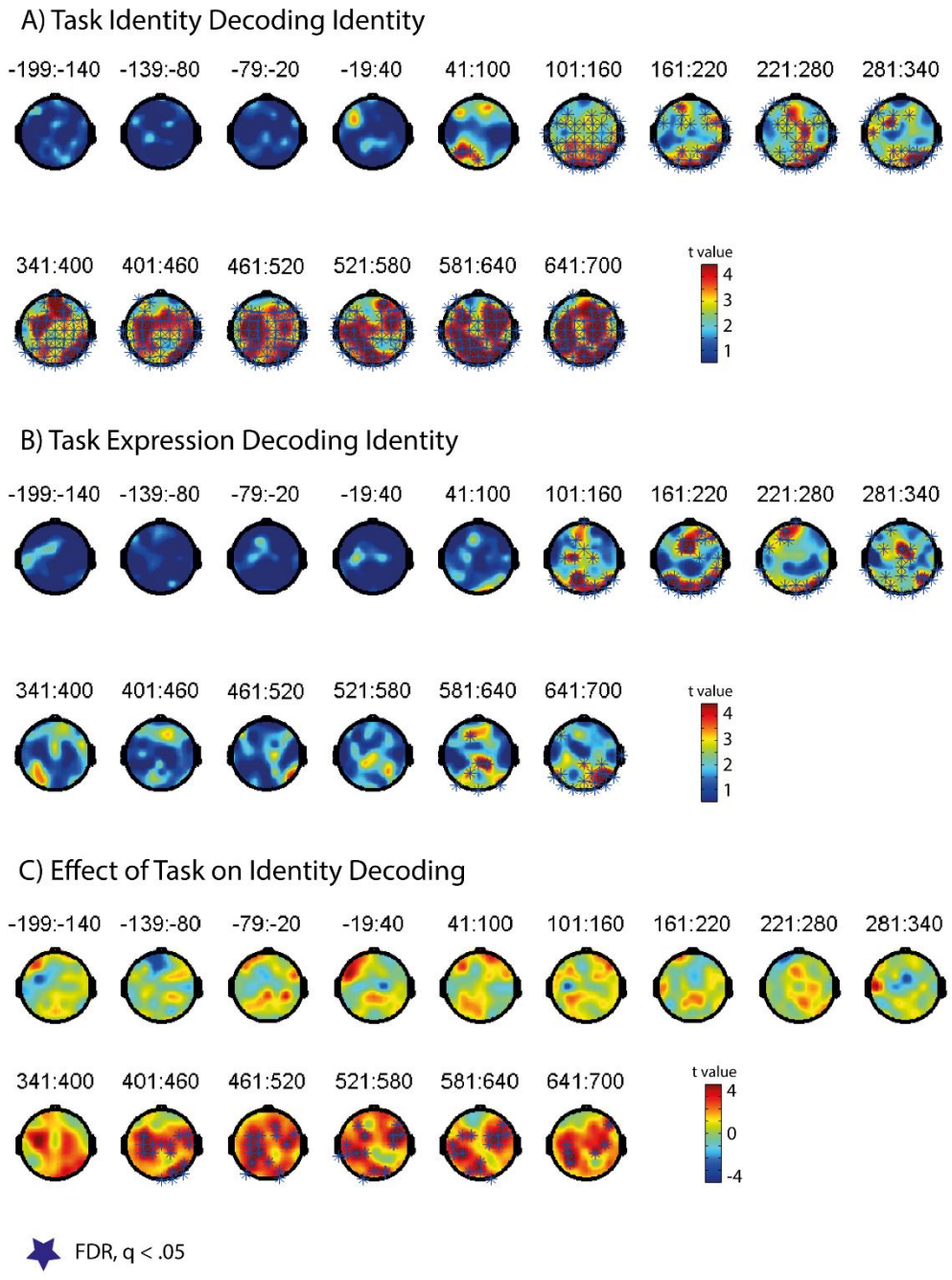


Figure 5: Spatially resolved identity decoding across tasks

Exemplar No.	Across expression (within identity)	Across identities (within expression)
1	4.29	7.50
2	4.78	7.34
3	5.02	7.44
4	5.76	6.61
5	4.90	7.30
6	6.46	6.70
7		7.30
Grand Mean	**5.21**	**7.17**

Supplementary Table 1: Low level stimulus properties

The table shows the mean Euclidean distance, calculated on a pixel wise basis from the images used in the experiment, across each expression (first column) for each identity in turn (exemplars 1-6), and the mean Euclidean distance across identities (second column) for each facial expression in turn (1-7). The grand means are reported at the bottom of the table. The data shows that identity is more easily discriminable from the low level stimulus properties than is expression and this holds for every exemplar considered.